Title: Productivity definition of the chilling requirement reveals underestimation of the impact of climate change on winter chill accumulation

Running head: bud break control by temperature in fruit trees

José Antonio Campoy[1], Rebecca Darbyshire[2,3], Elisabeth Dirlewanger[1], José Quero-García[1], Bénédicte Wenden[1]

[1]INRA, UMR Biologie du Fruit et Pathologie, Univ. Bordeaux, Villenave d'Ornon, France; [2]New South Wales Department of Primary Industries, Wagga Wagga, Australia. [3]Faculty of Veterinary and Agricultural Sciences, University of Melbourne, Melbourne, Australia

Corresponding author: benedicte.wenden@inra.fr (Tel: +33 5 57 12 25 49)

Keywords: *Prunus avium*, sweet cherry, flowering, temperature, chill, phenology, projections

Type of paper: Primary research article

Abstract

Evaluation of chilling requirements (CR) of cultivars of temperate fruit trees provides key information to assess regional suitability, according to winter chill, for both industry expansion and ongoing profitability as climate change continues. Traditional methods for calculating CR use climate controlled chambers and define CR using a fixed budburst percentage, usually close to 50% (CR-50%), without considering the productivity level associated to this percentage. This CR-50% definition may underestimate the real CR of tree crops for optimal productivity. This underestimation is particularly important to consider as winter chill accumulation is declining in many regions due to climate change. In this work we used sweet cherry to analyse the traditional method for calculating CR in many Rosaceae species (CR-50%) and compared the results with more a restrictive, productivity focused method, with CR defined with a 90% bud break level (90%, CR_m-90%) close to the optimal budburst which assures productivity. Climate projections of winter chill suitability across Europe using CR-50% and CR_m-90% were calculated. Regional suitability landscape was highly dependent on the method used to define CR and differences were found for a wide area of the European geography, both cold and mild winter areas. Our results suggest a need to use an optimal budburst level for the assessment of CR for sweet cherry. The use of traditional methods to determine CR can result in an underestimation of productivity CR with negative consequences for the fruit industry, particularly as climate change advances.

Introduction

Temperate deciduous fruit trees represent an important economic and food resource. Maintaining and expanding temperate fruit production is an industry priority and is likely to become more challenging under anthropogenic climate change. One aspect which will likely be influenced by climate change is sufficient accumulation of winter chilling (Luedeling *et al.*, 2011). In temperate fruit trees, the timing of bud break and flowering is highly correlated with a proper release of endodormancy, or rest, which is controlled by an accumulation of cold temperatures in winter (Saure, 1985). During this rest period, a certain amount of cold temperatures, defined as the chilling requirement, must be accumulated prior to the bud being released from endodormancy. Subsequent to this, the bud will respond to heat, leading to flowering and vegetative bud break (Lang *et al.*, 1987). This period of rest prevents bud break in response to conditions suitable for growth conditions, such as a warm spell in winter, which would then expose sensitive tissues to subsequent damaging cold conditions. The consequences of insufficient accumulation of chill to meet cultivar chilling requirements have been extensively studied. Insufficient chill can delay flowering and bud break, cause substantial damage to bud development including deformed buds (Petri & Leite, 2004; Viti *et al.*, 2008), and induce low levels of vegetative bud break and lack of uniformity of leafing and bloom (Samish, 1953; Erez & Couvillon, 1987; Erez, 2000). Within the context of climate change, these sub-optimal production outcomes may become more frequent. To predict such potential impacts, assist with orchard climate adaptation and guide breeding strategies, evaluation of cultivar specific chilling requirements (CR) is needed (Dennis, 2003; Campoy *et al.*, 2011; Chuine *et al.*, 2016).

Precise determination of the CR is not possible under field conditions. As such, various experimental methods have been used to evaluate dormancy depth (Cook *et al.*, 2017; Vitra *et al.*, 2017), date of dormancy release (Dennis, 2003; Castède *et al.*, 2014; Dantec *et al.*, 2014;

Chmielewski & Götz, 2016) and to assess the relationship between bud break and chilling and forcing temperatures (Harrington *et al.*, 2010; Luedeling & Gassner, 2012; Andreini *et al.*, 2014; Laube *et al.*, 2014). Forcing experiments using controlled climate chambers are commonly used to assess bud dormancy progression. This approach involves sampling tree cuttings through autumn and winter and evaluating bud break of the buds after they have been exposed to warm temperatures in a controlled climate chamber (Tabuenca, 1967; Dennis, 2003; Vitasse & Basler, 2014). In implementing this approach two main criteria have been used to determine CR; percentage of floral or vegetative bud break within a given period of time in the chamber (e.g. 50% break after 10 days) and the time required in the forcing chamber to reach a given stage of development (e.g. bud break) (Saure, 1985; Dennis, 2003). Of the two approaches, the former is often employed with the criteria to determine CR by allocating CR as when in-field chill accumulation leads to a 30-50% of bud break after 7 to 10 days in the forcing chamber (Hauagge & Cummins, 1991; Ruiz *et al.*, 2007; Viti *et al.*, 2010; Campoy *et al.*, 2012; Castède *et al.*, 2014). This criteria can vary by study with for instance, CR being determined using the emergence of only 3-4 flowers in the forcing chamber (Chmielewski & Götz, 2016; Götz *et al.*, 2017).

These criteria may not adequately represent CR that are required for profitable fruit production, in particular for crops which require high conversion of floral buds to fruit (e.g. cherry). These systems rely on high and consistent bud break rates which set a high production potential. Poor rates of floral and vegetative bud break, that is the proportion of floral and vegetative buds that truly open, can have a major impact on temperate fruit crop productivity (Erez, 2000). For small fruits, such as sweet cherry, a large number of viable flowers is required to reach commercial productivity, with a maximum bloom level desirable. Therefore, setting a CR value which only leads to 30-50% bud break may underestimate the CR needed for commercial profitability. This in turn will misjudge the potential impact of climate change on cherry production.

In this work, one of the most commonly employed forcing method in temperate fruit trees (in-field chilling required to lead to 50% bud break after 10 days forcing) was used to assess CR in sweet cherry and was contrasted with a modified method that sets a higher bud break percentage to better match requirements for commercial profitability. CR determined using both these methods were used to create climate change projections of the potential impact of insufficient chill accumulation in cherry across Europe. This work emphasizes the need to evaluate CR in terms of the minimum requirement of chill for commercially viability to best prepare industry and breeding programs for expansion and climate change.

Materials and methods

Bud break observations

Four sweet cherry cultivars were chosen for analysis encapsulating a presumed range in chilling requirements based on flowering dates (Fig. 1). The trees used for the experiments were grown following commercial-orchard cultural practices in the fruit tree experimental orchard of the Institut National de la Recherche Agronomique (INRA)-Bordeaux research center, located in Bourran, in Lot-et-Garonne (France, 44°19'N 0°24'E, 70m asl) and 60 km away in Toulenne, in Gironde (France, 44°34'N 0°16'W, 8m asl). Trees were grown on deep loamy soils, in mild winter regions with an average annual rainfall of 825 mm. Cultivars 'Cristobalina' and 'Regina' were grown in Bourran, 'Fertard' in Toulenne and 'Burlat' in both sites. Dates for beginning of flowering (5-10% open flowers, BBCH 61; Fadón *et al.*, 2015) and maturity (BBCH 89) were recorded for the four cultivars between 2000 and 2017.

Each fortnight between 1st September and 8th April (2015-2016 and 2016-2017 seasons, except for 'Cristobalina' that was sampled only in 2015-2016), two or three branches bearing floral buds were randomly cut from the two trees per cultivar and placed in a climate-controlled chamber under forcing conditions (25°C, 16h light/8h dark). Branches were discarded when buds were dry and/or necrotic, or when the proportion of open buds reached a plateau. Every two or three days the total number of floral buds that reached BBCH stage 55 (Fadón *et al.*, 2015) was recorded. Bud break percentage was recorded as the percentage of flower buds at stage 55 in relation to the total number of floral buds on the branches.

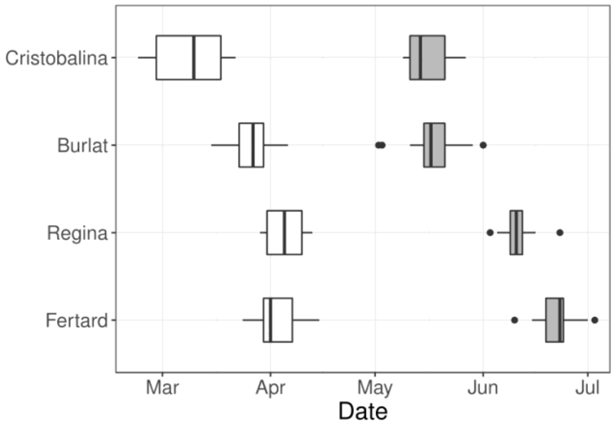

Fig. 1 Range of flowering (white boxes) and maturity (grey boxes) dates for the four studied cultivars (2000 – 2017).

Chill and heat accumulation estimation

For the assessment of chill and heat accumulation, hourly mean temperatures were collected from the local weather stations (years 2015-2017, INRA CLIMATIK, https://intranet.inra.fr/climatik, stations 47038002 and 33533002).

Chill accumulation, namely chill portions (CP), was calculated using the Dynamic chill model (Fishman *et al.*, 1987), which has previously been found to be the best fitting chill model among several tested models (Alburquerque *et al.*, 2008; Luedeling *et al.*, 2009a). For heat accumulation, the growing degree hours (GDH) model was used (Anderson *et al.*, 1986). Chill was accumulated from October 1st until the sampling date. For climate projection analyses chill was accumulated between October 1st and March 31st.

To assess CR, two methods were used. Firstly, the commonly used approach which defined CR as the field accumulated chill which leads to 50% of the buds above stage BBCH 55 after 10 days in forcing conditions (Ruiz *et al.*, 2007; Alburquerque *et al.*, 2008; Campoy *et al.*, 2012;

Sánchez-Pérez *et al.*, 2012; Azizi Gannouni *et al.*, 2017), hereby referred as CR-50%. For this study, the second method used a similar approach but set a higher bud break requirement, 90%, estimated as the maximum bud break percentage recorded after a prolonged forcing period (2-3 weeks), named here CR_m-90%.

Climatic and projection models data

The R package ChillR (Luedeling *et al.*, 2013) was used to generate hourly temperatures from daily maximum and minimum temperatures which uses a sine curve and a logarithmic function for day-time and night-time temperatures, respectively. For the climate projection analyses, two European temperature gridded datasets were used. Two regional climate datasets for historical and projected temperature made available by EURO-CORDEX (http://www.euro-cordex.net; Jacob *et al.*, 2014): MOHC-HadGEM2-ES and NOAA-GFDL-GFDL-ESM2M, r1i1p1 ensemble, regionalized using the SMHI-RCA4 regional change model (50 km resolution, EUR-44) were used for the assessment. Two emission scenarios (RCP 4.5 and RCP 8.5) were assessed for each climate model. We corrected the differences for the temperatures between euro-cordex projections and recorded data using the E-OBS gridded temperature dataset with 0.25° resolution (v.14; Haylock *et al.*, 2008). Gridded annual chill accumulation values were calculated for the three data sets (E-OBS, MOHC-HadGEM2_ES and NOAA-GFDL-GFDL-ESM2M) for 1978-2005 and the average anomaly grid, defined as the difference between E-OBS and RCM datasets, was added to the chill accumulation grids calculated for the four RCM datasets (RCP 4.5 and RCP 8.5).

Safe winter chill (SWC; Luedeling *et al.*, 2009b) was used to estimate whether future European winter chilling conditions will likely be suitable for each cultivar and based on the CR estimated using the two methods. SWC is the amount of winter chill that can be reliably expected in 90% of all years, or the 10th percentile of the dataset. This metric is meaningful to fruit producers, because failure to meet chilling requirements in more than 10% of years is likely to render production uneconomical (Luedeling *et al.*, 2009b).

Results

Bud break percentage based on chill accumulation

Bud break response to field accumulated chill prior to cuttings being taken was evaluated (Fig. 2). Low - but not nil - bud break percentages were observed for branches that had been sampled in the early season (mid-November), suggesting that early (‘Cristobalina’) and mid-flowering (‘Burlat’) cultivars could respond to warm temperatures after the accumulation of only 13 CP. Although only a low percentage of bud break was observed (i.e. less than 5%). As more chill was accumulated in the field, the rate of floral bud break increased and the maximum bud break percentage, marked by the plateau for each line, was higher (Fig. 2). These results indicate that the amount of accumulated chill primarily drives bud break percentages as the buds were all exposed to similar levels of forcing temperatures (Fig. 2).

The bud break percentage to accumulated chill did notably differ between cultivars, not only in the rate of bud break with increasing chill but also in the final percentage of bud break (Figs 2 and 3). For example, the early flowering cultivar ‘Cristobalina’ (i.e. low-chill cultivar) was found to have higher bud break potential (45% bud break) after low levels of accumulated chill (32 CP) whereas the late flowering (i.e. high-chill cultivar) cultivar ‘Regina’ only reached 14.5% bud break after accumulating 32 CP. For the late flowering cultivars to meet the equivalent 45% bud break, 53 CP and 65 CP were needed for ‘Regina’ and ‘Fertard’, respectively. This pattern was also found for the capacity to reach high bud break percentage. After accumulating 40 CP, ‘Cristobalina’ and ‘Burlat’ reached 100% and 84% bud break respectively whereas late flowering cultivars (‘Regina’ and ‘Fertard’) only reached 28% and 16% bud break, respectively (Fig. 3, Fig. S1). These differences are also noticeable for the bud ability to respond to forcing conditions as revealed by the rate of bud break (Fig. 2). For example, for 'Burlat', bud break percentage increase markedly faster for branches that have accumulated at least 90 CP than for branches sampled earlier during chill accumulation.

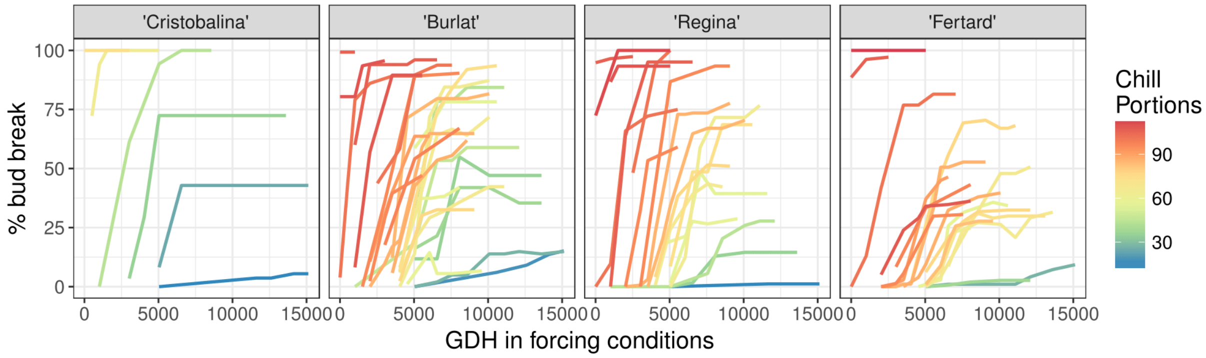

Fig. 2 Floral bud break percentage for the four cultivars with various field chill accumulation values (in chill portions). Note that no results for 'Cristobalina' were recorded for chill accumulation greater than 69 CP as bud burst had begun in the field. GDH: growing degree hours.

Chilling requirement calculation

The chilling requirement for each cultivar was evaluated using the common approach (CR-50%; Fig. 3). Values calculated this way were highly variable between years with, for example, values of 77 to 91 CP found for 'Burlat' (Fig. 3, Table 1). CR were also calculated using a 90% bud break threshold (CR_m-90%). Values for CR_m-90% ranged between 42 CP for 'Cristobalina' and 110 CP for 'Fertard' (Fig. 3, Table 1).

Taking the average chill portion accumulation to reach 50% and 90% bud break, CR for each cultivar were estimated (Table 1). CR differs with cultivar and by the method used to evaluate it but the CR estimated by CR_m-90% are all higher than CR-50%.

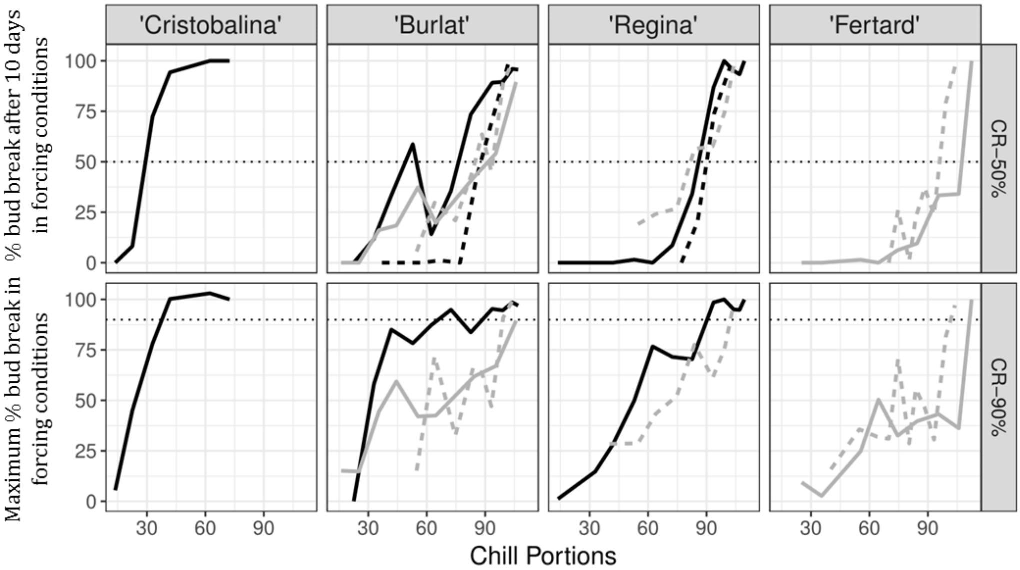

Fig. 3 Bud break data used to calculate CR-50% and CRM-90%. Upper panel: bud break percentage after 10 days under forcing conditions; lower panel: maximal bud break percentage reached under forcing conditions. Horizontal dotted lines represent the 50% and 90% thresholds for CR-50% and CR_m-90% respectively. Black and grey lines represent data for cultivars grown in Bourran and Toulenne, respectively. Solid lines are for 2015-2016 data while dashed lines are for 2016-2017 data.

Table 1 Average chill requirement values differ between the four cultivars and the method used to calculate CR.

	CR-50%	CR_m-90%
'Cristobalina'	29 CP	42 CP
'Burlat'	86 CP (±5)	92 CP (±15)
'Regina'	86 CP (±3)	99 CP (±5)
'Fertard'	101 CP (±5)	108 CP (±4)

Future production risk due to insufficient chill

The risk of insufficient chill accumulation for each cultivar based on the two methods to determine CR (Table 1) was estimated across Europe using two different climatic models and two emission scenarios (Figs 4, 5, S2 and S3). We focused on MOHC-HadGEM2-ES, rcp8.5, projecting the highest increase in temperatures (most pessimistic; Fig. 4) and NOAA-GFDL-GFDL-ESM2M, rcp4.5, projecting the lowest increase in temperatures (most optimistic; Fig. 5). Areas defined in Figures 4 and 5 reveal that for the four cultivars, the regions at risk of not meeting CR increase substantially out to 2075-2100 using both estimations of CR (CR-50% and CR_m-90%). The area at risk is larger for CR_m-90% than for CR-50% in both scenarios. Areas coloured in pink, show the areas meeting CR-50% but not CR_m-90% (Figs 4 and 5). Therefore, pink areas show the difference of estimated potential risk of insufficient chill depending on the method used to define CR (either CR-50% or CR_m-90%). The difference in risk based on CR methodology is especially evident for the high-chill cultivar ‘Regina’. Under both scenarios, a large area of Europe will not meet CR_m-90% whereas using CR-50% a much lower area of impact was found (Figs 4 and 5). For example, when considering CR-50%, sweet cherry production in United Kingdom appears assured for all cultivars whereas late cultivars as ‘Regina’ may not receive enough chill to guarantee optimal bud break by 2075-2100. In the same line, Eastern European areas and Anatolia will not receive enough chilling for a high-chill cultivar such as ‘Regina’. For an extra-low chill cultivar, such as ‘Cristobalina’, CR-50% will be met in almost all the Mediterranean basin, but chilling to fulfil CR_m-90% may not be guaranteed in some areas of Southern Italy, Southern Spain and Northern Africa for 2026-2100.

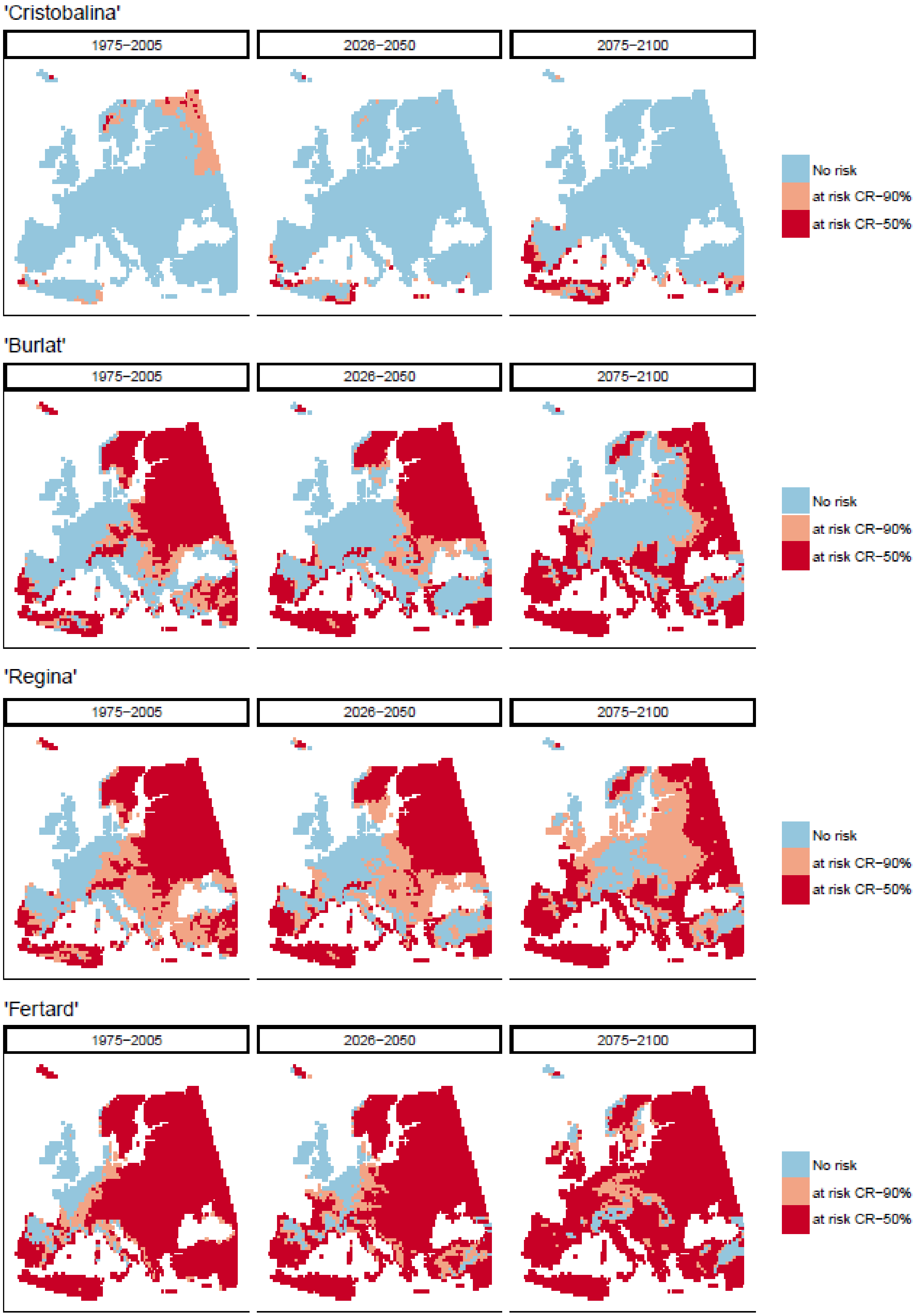

Fig. 4 European maps showing where safe winter chill (10th percentile) will not meet chilling requirements as estimated by forcing experiments (CR-50%; red areas) and by optimal bud break rate (CR_m-90%; pink and red areas) for the four cultivars. Blue indicates CR will be met for both CR values. Thresholds for the chilling

requirements calculated in Table1 were used. Scenario MOHC-HadGEM2-ES, rcp8.5, projects the highest increase in temperatures (most pessimistic).

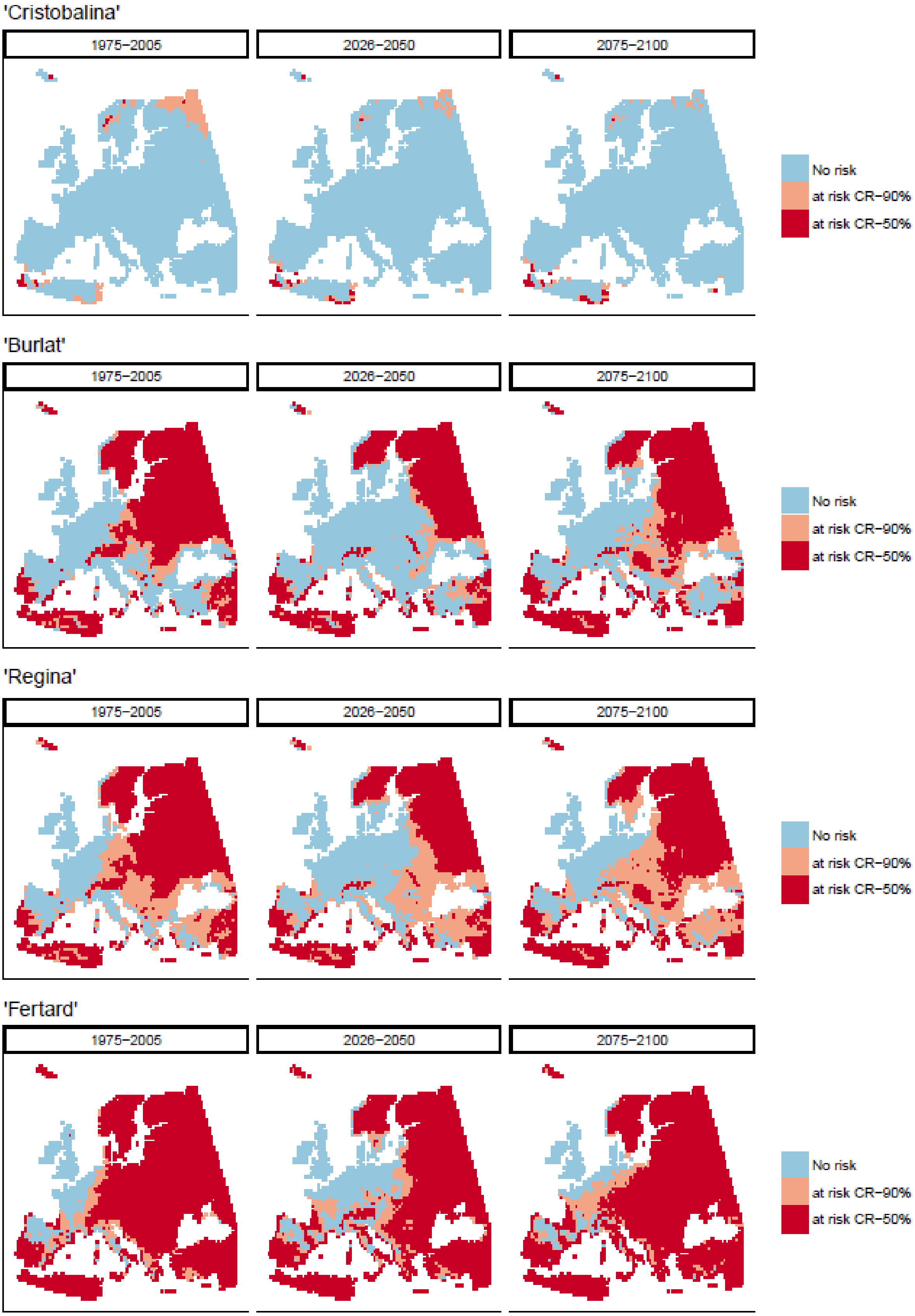

Fig. 5 European maps showing where safe winter chill (10th percentile) will not meet chilling requirements as estimated by forcing experiments (CR-50%; red areas) and by optimal bud break rate (CRm-90%; pink and red areas) for the four cultivars. Blue indicates CR will be met for both CR values. Thresholds for the chilling requirements calculated in Table1 were used. Scenario NOAA-GFDL-GFDL-ESM2M, rcp4.5, projects the lowest increase in temperatures (most optimistic).

Discussion

Bud break percentage in response to chill accumulation

We evaluated bud break responses to various levels of in-field chill accumulation using forcing experiments on cultivars with contrasting chill requirements. The rate of bud break gradually increased with in-field accumulated chill, thus confirming that chill primarily drives the capacity of the buds to burst, but with contrasted responses for the different cultivars. Following these observations, greater chill accumulation increased the maximum bud break percentage but with a different response between cultivars (Fig. 3). Overall, the results indicate that the amount of accumulated chill can greatly limit the percentage of bud break even under optimal growth conditions as illustrated by the response to chill and heat accumulation (Fig. S1). This is especially true of the early flowering cultivar ‘Cristobalina’ which shows a very strict control of bud break potential by the amount of chill accumulated with limited effect of heat accumulation (Fig. 4; Fig. S1). In addition, according to our data, there is a limit to the effect of heat on the bud break percentage. When bud break percentages were considered as a response to chill and heat accumulation (Fig. S1), results suggest that for a given chill accumulation bud break might never reach 100%. For example, bud break percentage in ‘Regina’ fails to reach 60% if chill accumulation is under 60 CP regardless of the level of heat accumulated. This provides a clear chill requirement limit to obtain maximum bud break percentage suitable for commercial growing of sweet cherry.

The interaction of chilling with heat requirements and bud break was also shown in different temperate *Rosaceae*: cherry (Measham *et al.*, 2017), peach (Couvillon & Erez, 1985; Okie & Blackburn, 2011), sour cherry (Felker & Robitaille, 1985), apple (Powell, 1986) and pear (Spiegel-Roy & Halston, 1979); and in a notable group of forest species (Laube *et al.*, 2014). This interaction has been associated to a 'residual effect of dormancy' (Erez, 2000), a parameter indicating the distance to optimal chilling, and therefore, productivity (Okie & Blackburn, 2011). This term is used when crops show symptoms of insufficient chilling (e.g. deficient bud break or fruit set and uneven foliation) even after satisfaction of their CR, usually corresponding to CR-30% or CR-50% (Campoy *et al.*, 2011). Therefore, increasing the required bud break percentage when assessing CR will provide a more reliable measure of profitable CR.

Considering previous results reported in other temperate fruit species such as apricot (Viti *et al.*, 2010; Campoy *et al.*, 2012), peach (Romeu *et al.*, 2014), Japanese plum (Ruiz *et al.*, 2017), almond (Egea *et al.*, 2003), apple and pear (Hauagge & Cummins, 1991); the proposed CR based on a commercial requirement of bud break (e.g. 90%), could be applied in these temperate fruit species. The use of CR based on bud break for the assessment of regional suitability (determining the match of a growing area and cultivars or species) would minimize the productivity problems associated to the 'residual effect of dormancy', insufficient fulfilment of optimal chilling requirements. It would not be advisable to choose a CR-100%. A small percentage should be given as buffer for minor physiological problems or accidental bud drop during the manipulation of plant material on growth chambers.

Chilling requirements calculation

The chill accumulation necessary to reach 90% (CR_m-90%) of flower bud break was found to be considerably higher than the chilling requirements estimated with the common forcing method (CR-50%) as shown in Table 1 (Dennis, 2003; Campoy *et al.*, 2011; Measham *et al.*, 2017). This reflects that the traditional assessment of chilling requirements may underestimate the real requirement to reach commercial productivity. In the case of commercially grown trees, the fulfilment of CR also needs to be “constant over years” to assure productivity and economic viability. Thus, this underestimation of CR is very important for both high and low chill cultivars in the context of climate change. The underestimation of CR could be considered trivial for temperate areas characterized by cold winters, when chill accumulation in the field normally exceeds the CR of cultivars, as both CR-50% and CR_m -90% are easily achieved. However, climatic projections (Figs. 4 and 5, Luedeling *et al.*, 2011) for cold areas show that high-chill cultivars may experience productivity problems by the end of the century. For locations where CR of a given cultivar are rarely achieved, the use of CR-50% instead of CR_m-90% will likely have a more significant impact. The underestimation of CR could lead to a higher probability and frequency of productivity problems due to insufficient chilling fulfilment. This is also true for low-chill cultivars that are grown in mild winter climates which are usually oriented to the profitable early-market (Egea *et al.*, 2010). In areas which are currently susceptible to insufficient chill, dormancy breaking agents can be used to compensate for insufficient chilling (Erez, 2000). Greater understanding of these agents ability to compensate for insufficient under climate change is required to understand if these provide an enduring adaptation strategy.

In the current climate change context, the risk of insufficient chill accumulation will increase. To more broadly understand the risk warming will pose to fruit tree production, we propose the evaluation of chilling requirements using higher percentages of bud break (around 90%) over a longer period under forcing conditions for crop with a high bloom load need for profitability. This approach should be undertaken to assess chilling requirements for the evaluation of new cultivars. This agrees with the work from Measham et al. (2017) on the impact of the method for determining chill requirement on practical decision-making in the orchard, and on the assessment of regional suitability in warm-winter areas of Australia.

Future production risk due to insufficient chill

The projected chill accumulation data together with the projected bud break potential shown in this study provide new evidence of climate change risks for the cultivation of sweet cherry across Europe. This risk increases with the chilling requirement of the cultivar and the method used to calculate it (CR-50% or CR_m-90%). In the Mediterranean basin (a marginal chill area), only extra-low chill cultivars, such as 'Cristobalina', will have regional suitability for its cultivation along the 21st century. However, for high-chill cultivars, regional suitability restriction is extended to almost the whole of the continental Europe, especially using the CRM-90% estimation (as shown in Figs. 4 and 5). Thus, the underestimation of chilling requirements together with the loss of chill in future time periods provide a warning message of the sustainability of temperate fruit production and urge breeders for the development of cultivars adapted to the upcoming climatic conditions. This is especially sound for species for which no low-chill cultivars have been bred so far, such as sweet cherry and apricot.

Climate change: a shift in growing areas and cultivars.

For the most pessimistic scenarios (rcp 8.5, Fig. 4), the projections show notable problems for chill fulfilment of high chill cultivars in areas currently considered as sufficiently cold, i.e. Northern Europe and British Isles. This highlights that high chill cultivars will need to be replaced with lower chill cultivars. Interestingly, new areas suitable for cultivars with relatively high chill requirements appear in North-Eastern Europe by the end the century. Although this may seem counterintuitive, most models of chill consider that temperatures below 0/-2°C are not effective for chill accumulation since they might inhibit all cellular functions (e.g. Fishman *et al.*, 1987; Hänninen, 1990). Consequently, current climatic conditions are too cold to satisfy chill requirements will improve in suitability for chill accumulation and illustrates new production areas suitable for fruit tree cultivation.

Overall, this paper reveals that the method used to assess chilling requirements does have an important impact on the projection of regional and cultivar suitability of sweet cherry. The underestimation of CR due to experimental method could also have an important impact for the assessment of other temperate fruit crops, considering the similarity of methods used to assess CR and the analogy of dormancy and flowering processes. Therefore, this work highlights the need to carefully evaluate chill requirements in order to assess the future production risk and possible shifts in temperate fruit tree growing areas in Europe due to climate change.

Acknowledgements

The authors would like to acknowledge the E-OBS dataset from the EU-FP6 project ENSEMBLES (http://ensembles-eu.metoffice.com) and the data providers in the ECA&D project (http://www.ecad.eu). JAC was supported by CEP Innovation and Aquitaine Region (AQUIPRU project 2014-1R201022971). The authors warmly thank Teresa Barreneche, Hélène Christmann, Jacques Joly, Lydie Fouilhaux, Noémie Vimont and Rémi Beauvieux for collecting the branches and collaborating on the phenotyping. The authors thank the INRA's '*Prunus* Genetic Resources Center' for preserving and managing the sweet cherry collections and the Fruit Experimental Unit of INRA-Bordeaux (UEA) for growing the trees and managing the orchards.

References

Alburquerque N, García-Montiel F, Carrillo A, Burgos L (2008) Chilling and heat requirements of sweet cherry cultivars and the relationship between altitude and the probability of satisfying the chill requirements. *Environmental and Experimental Botany*, **64**, 162–170.

Anderson J, Richardson E, Kesner C (1986) Validation of chill unit and flower bud phenology models for'Montmorency'sour cherry. *Acta Horticulturae*, **184**, 71–78.

Andreini L, De Cortázar-Atauri IG, Chuine I et al. (2014) Understanding dormancy release in apricot flower buds (*Prunus armeniaca* L.) using several process-based phenological models. *Agricultural and Forest Meteorology*, **184**, 210–219.

Azizi Gannouni T, Campoy JA, Quero-García J, Barreneche T, Arif A, Albouchi A, Ammari Y (2017) Dormancy related traits and adaptation of sweet cherry in Northern Africa: A case of study in two Tunisian areas. *Scientia Horticulturae*, **219**, 272–279.

Campoy J a., Ruiz D, Egea J (2011) Dormancy in temperate fruit trees in a global warming context: A review. *Scientia Horticulturae*, **130**, 357–372.

Campoy JA, Ruiz D, Allderman L, Cook N, Egea J (2012) The fulfilment of chilling requirements and the adaptation of apricot (*Prunus armeniaca* L.) in warm winter climates: An approach in Murcia (Spain) and the Western Cape (South Africa). *European Journal of Agronomy*, **37**, 43–55.

Castède S, Campoy JA, Quero-García J et al. (2014) Genetic determinism of phenological traits highly affected by climate change in *Prunus avium*: flowering date dissected into chilling and heat requirements. *The New phytologist*, **202**, 703–15.

Chmielewski F-M, Götz K-P (2016) Performance of models for the beginning of sweet cherry blossom under current and changed climate conditions. *Agricultural and Forest Meteorology*, **218–219**, 85–91.

Chuine I, Bonhomme M, Legave J-M, García de Cortázar-Atauri I, Charrier G, Lacointe A, Améglio T (2016) Can phenological models predict tree phenology accurately in the future? The unrevealed hurdle of endodormancy break. *Global Change Biology*, **22**, 3444–3460.

Cook NC, Calitz FJ, Allderman LA, Steyn WJ, Louw ED (2017) Diverse patterns in dormancy progression of apple buds under variable winter conditions. *Scientia Horticulturae*, **226**, 307–315.

Couvillon GA, Erez A (1985) Influence of prolonged exposure to chilling temperatures on bud break and heat requirement for bloom of several fruit species. *J. Am. Soc. hort. Sci.*, **110**, 47–50.

Dantec CF, Vitasse Y, Bonhomme M, Louvet J-M, Kremer A, Delzon S (2014) Chilling and heat requirements for leaf unfolding in European beech and sessile oak populations at the southern limit of their distribution range. *International journal of biometeorology*, **58**, 1853–1864.

Dennis F (2003) Problems in standardizing methods for evaluating the chilling requirements for the breaking of dormancy in buds of woody plants. *Hort Science*, **38**, 347–350.

Egea J, Ortega E, Martinez-Gomez P, Dicenta F (2003) Chilling and heat requirements of almond cultivars for flowering. *Environmental and Experimental Botany*, **50**, 79–85.

Egea J, Rubio M, Campoy JA et al. (2010) “Mirlo Blanco”, “Mirlo anaranjado”, and “Mirlo Rojo”: Three new very early-season apricots for the fresh market. *HortScience*, **45**, 1893–1894.

Erez A (2000) Bud Dormancy; Phenomenon, Problems and Solutions in the Tropics and Subtropics. In: *Temperate Fruit Crops in Warm Climates*, pp. 17–48.

Erez A, Couvillon GA (1987) Characterization of the moderate temperature effect on peach bud rest. *J. Am. Soc. hort. Sci.*, **112**, 677–680.

Fadón E, Herrero M, Rodrigo J (2015) Flower development in sweet cherry framed in the BBCH scale. *Scientia Horticulturae*, **192**, 141–147.

Felker FC, Robitaille HA (1985) Chilling accumulation and rest of sour cherry flower buds. *J.*

Am. Soc. Hortic. Sci., **110**, 227–232.

Fishman S, Erez A, Couvillon GA (1987) The temperature dependence of dormancy breaking in plants: Mathematical analysis of a two-step model involving a cooperative transition. *Journal of Theoretical Biology*, **124**, 473–483.

Götz KP, Chmielewski FM, Gödeke K et al. (2017) Assessment of amino acids during winter rest and ontogenetic development in sweet cherry buds (*Prunus avium* L.). *Scientia Horticulturae*, **222**, 102–110.

Hänninen H (1990) Modelling bud dormancy release in trees from cool and temperate regions. *Acta Forestalia Fennica*, **213**, 1–47.

Harrington CA., Gould PJ, St.Clair JB (2010) Modeling the effects of winter environment on dormancy release of Douglas-fir. *Forest Ecology and Management*, **259**, 798–808.

Hauagge R, Cummins JN (1991) Seasonal variation in intensity of bud dormancy in apple cultivars and related *Malus* species. *Journal of the American Society for Horticultural Science*, **116**, 107–115.

Haylock MR, Hofstra N, Klein Tank AMG, Klok EJ, Jones PD, New M (2008) A European daily high-resolution gridded data set of surface temperature and precipitation for 1950-2006. *Journal of Geophysical Research Atmospheres*, **113**, D20119.

Jacob D, Petersen J, Eggert B et al. (2014) EURO-CORDEX: New high-resolution climate change projections for European impact research. *Regional Environmental Change*, **14**, 563–578.

Lang G, Early J, Martin G, Darnell R (1987) Endo-, para-, and ecodormancy: physiological terminology and classification for dormancy research. *Hort Science*, **22**, 371–377.

Laube J, Sparks TH, Estrella N, Höfler J, Ankerst DP, Menzel A (2014) Chilling outweighs photoperiod in preventing precocious spring development. *Global change biology*, **20**, 170–82.

Luedeling E, Gassner A (2012) Partial Least Squares Regression for analyzing walnut phenology in California. *Agricultural and Forest Meteorology*, **158–159**, 43–52.

Luedeling E, Zhang M, Luedeling V, Girvetz EH (2009a) Sensitivity of winter chill models for fruit and nut trees to climatic changes expected in California's Central Valley. *Agriculture, Ecosystems & Environment*, **133**, 23–31.

Luedeling E, Zhang M, Girvetz EH (2009b) Climatic changes lead to declining winter chill for fruit and nut trees in California during 1950-2099. *PLoS ONE*, **4**.

Luedeling E, Girvetz EH, Semenov MA., Brown PH (2011) Climate change affects winter chill for temperate fruit and nut trees. *PLoS ONE*, **6**.

Luedeling E, Kunz A, Blanke MM (2013) Identification of chilling and heat requirements of cherry trees-a statistical approach. *International journal of biometeorology*, **57**, 679–89.

Measham PF, Darbyshire R, Turpin SR, Murphy-White S (2017) Complexity in chill calculations: A case study in cherries. *Scientia Horticulturae*, **216**, 134–140.

Okie WR, Blackburn B (2011) Increasing chilling reduces heat requirement for floral budbreak in peach. *HortScience*, **46**, 245–252.

Petri JL, Leite GB (2004) Consequences of Insufficient Winter Chilling on Apple Tree Bud-break. *Acta Horticulturae*, **662**, 53–60.

Powell LE (1986) The chilling requirement in apple and its role in regulating time of flowering in spring in cold-winter climates. *Acta Horticulturae*, **179**, 1–11.

Romeu JF, Monforte AJ, Sánchez G, Granell A, García-Brunton J, Badenes ML, Ríos G (2014) Quantitative trait loci affecting reproductive phenology in peach. *BMC plant biology*, **14**, 52.

Ruiz D, Campoy JA, Egea J (2007) Chilling and heat requirements of apricot cultivars for flowering. *Environmental and Experimental Botany*, **61**, 254–263.

Ruiz D, Guevara-Gazquez A, García F, Carrilo-Navarro A, Cos-Terrer J (2017) New Japanese plum (*Prunus salicina* L.) breeding program in Murcia (Spain). *Acta Horticulturae*, **1172**, 123–134.

Samish RM (1953) Dormancy in woody plants. *Annual Review of Plant Physiology*, **5**, 183–204.

Sánchez-Pérez R, Dicenta F, Martínez-Gómez P (2012) Inheritance of chilling and heat requirements for flowering in almond and QTL analysis. *Tree Genetics and Genomes*, **8**, 379–389.

Saure M (1985) Dormancy release in deciduous fruit trees. *Horticultural reviews*, **7**, 239–299.

Spiegel-Roy P, Halston FH (1979) Chilling and Post-Dormant Heat Requirement as Selection Criteria for Late-Flowering Pears. *Journal of horticultural science*, **54**, 115–120.

Tabuenca M (1967) Necesidades de frio invernal de variedades deciruelo. *An Aula Dei*, **8**, 383–391.

Vitasse Y, Basler D (2014) Is the use of cuttings a good proxy to explore phenological responses of temperate forests in warming and photoperiod experiments? *Tree physiology*, **34**, 174–83.

Viti R, Bartolini S, Andreini L (2008) Apricot Flower Bud Development : Main Biological , Physiological and Environmental Aspects Related to the Appearance of Anomalies. *International Journal of Plant Developmental Biology*, **2**, 25–34.

Viti R, Andreini L, Ruiz D, Egea J, Bartolini S, Iacona C, Campoy JA (2010) Effect of climatic conditions on the overcoming of dormancy in apricot flower buds in two Mediterranean areas: Murcia (Spain) and Tuscany (Italy). *Scientia Horticulturae*, **124**, 217–224.

Vitra A, Lenz A, Vitasse Y (2017) Frost hardening and dehardening potential in temperate trees from winter to budburst. *New Phytologist*, **216**, 113–123.